THE MEDULLARY RAYS OF CEDRUS

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(WITH SEVEN FIGURES)

In those conifers the medullary rays of which are provided with marginal cells, it is commonly found that marginal tracheids in the xylem region of a ray are conterminous with the so-called "erect cells" in the phloem region of the ray. Such a condition was figured for *Pinus sylvestris* by STRASBURGER in his notable contributions to the anatomy of the conducting system (5), and the figure is copied in his textbook (6). It has in fact been claimed by more recent writers (7) that the marginal tracheids and the erect cells are corresponding structures, just as are ordinary tracheids and sieve tubes. It was accordingly with some surprise that the writer observed, in the course of a study of the origin of erect cells (1), that in the genus *Cedrus* erect cells were conterminous with parenchyma cells in the xylem region of a ray. An insufficient supply of material was at that time available, but recently this lack has been liberally supplied through the kindness of Miss R. HOLDEN of Cambridge University, Mr. R. I. LYNCH, Director of the Cambridge Botanical Garden, Professor E. C. JEFFREY of Harvard University, and Mr. H. N. LEE, formerly of the same institution. From these sources material of all three species of *Cedrus* and of the related monotypic genus *Pseudolarix* has been received, and it is now possible to give an interpretation of the anomalous features of *Cedrus* wood, and to offer evidence as to the relationships of the genus.

In a general way the wood of *Cedrus* bears much resemblance to that of *Abies*, but differs in having more numerous resin cells at the outer edge of annual rings, and in showing ray tracheids, which are, however, mixed with marginal parenchyma. Marginal cells are typically much less abundant than in *Pinus* and other Pineae; in *Cedrus* some rays lack marginal cells, while others are devoid of such cells for considerable distances. STRASBURGER (5) has called

attention to the fact that in this genus marginal tracheids occur with uncertainty, and concludes that they are generally more abundant in the mature trunk than in young branches, although they are sometimes scarce in the trunk.

A study of young stems and roots, and of older specimens where the phloem region is preserved, shows that when marginal cells are present in the xylem they are continuous with erect cells in the phloem, but that the latter are frequently present when the xylem

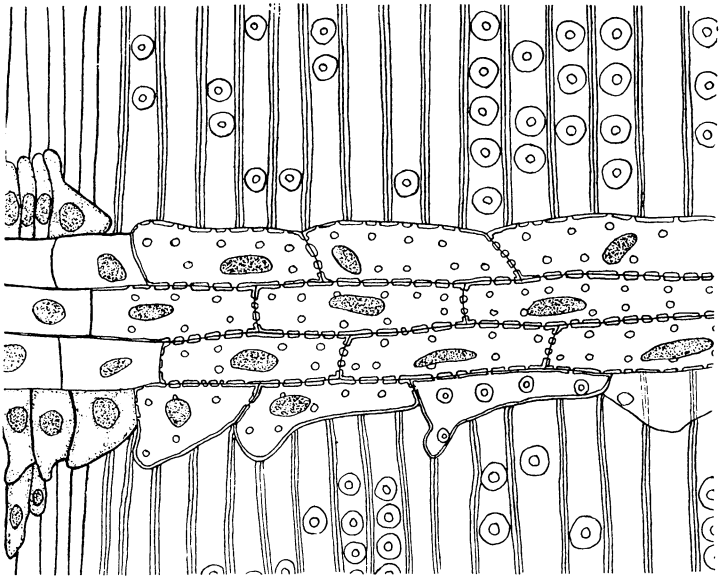

FIG. 1.—*Cedrus deodar*, stem; radial section through twelfth growth ring of xylem, with cambium and a small portion of phloem; in this and the succeeding figures the axis of the stem (or root) lies toward the right; ×290.

has no marginal cells. In such cases a triangular cambial cell occurs at the edge of the ray, as is shown in fig. 1, taken from a twelve-year old branch of *Cedrus deodar*. But in cases where such a medullary ray can be traced through several annual rings, it may generally be made out that scattered marginal cells occur, especially at the end of a year's growth, as may be seen in fig. 2, which represents a continuation of the section shown in fig. 1. Both margins of the ray in question show not only the scattered occur-

rence of the marginal cells, but the mixture of tracheids and parenchyma cells constituting the marginal row. The parenchyma of the marginal rows, like that of the central rows, is more or less completely filled with starch grains, which have been omitted from the figures for the sake of clearness. In some instances the marginal cells are practically restricted to the region of the end of an annual ring, and in such cases the marginal cells are entirely of a parenchymatous nature, as is shown in fig. 3, which is taken from

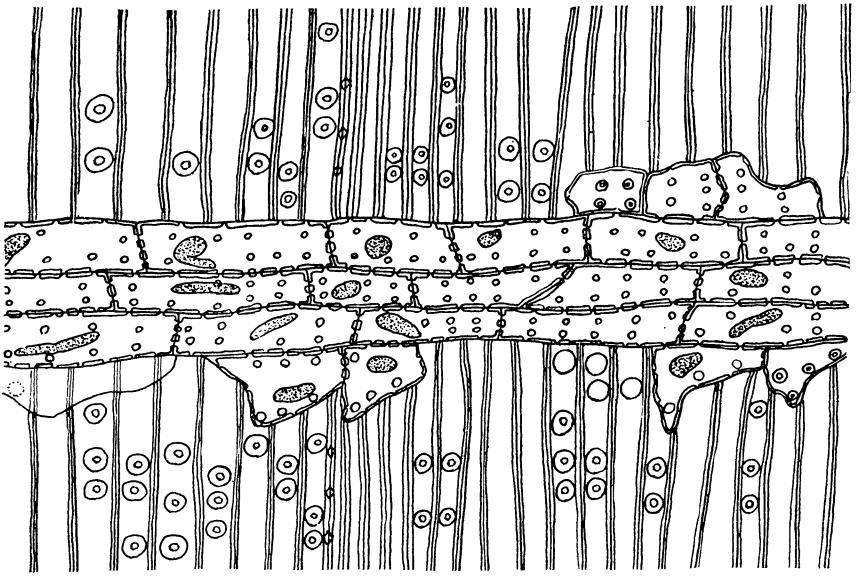

FIG. 2.—*C. deodar*, stem; a continuation of fig. 1, as may be seen from the presence of a shadowy cell on the lower margin of the ray in both figures; ×290.

near the cambial region of a root of *C. libani*. In this and other figures is to be seen the unusual shape of the marginal cells, which are triangular or pointed or tailed. It will be recalled that in most genera which possess marginal cells these are rectangular cells elongated in the radial direction, as are the central cells of a ray.

The lower margin of the ray shown in fig. 2 contains one of the shadowy cells or "ghosts" referred to by THOMPSON (**7**, **8**) as characteristic of *Abies*, and considered by him to represent an

advanced stage of degeneration of marginal cells. These "ghosts" are of very frequent occurrence in the three species of *Cedrus*.

Another common feature of the marginal row is shown in fig. 4, from a root of *C. libani*, where a solitary cell containing rhombic crystals of calcium oxalate appears at the end of an annual ring, a situation which is quite the rule, though not invariable. Crystal-containing cells may also be found among the erect cells of the phloem region of a ray, as is shown in fig. 5. The occurrence of crystals in the phloem parenchyma is universal in *Cedrus*, as in

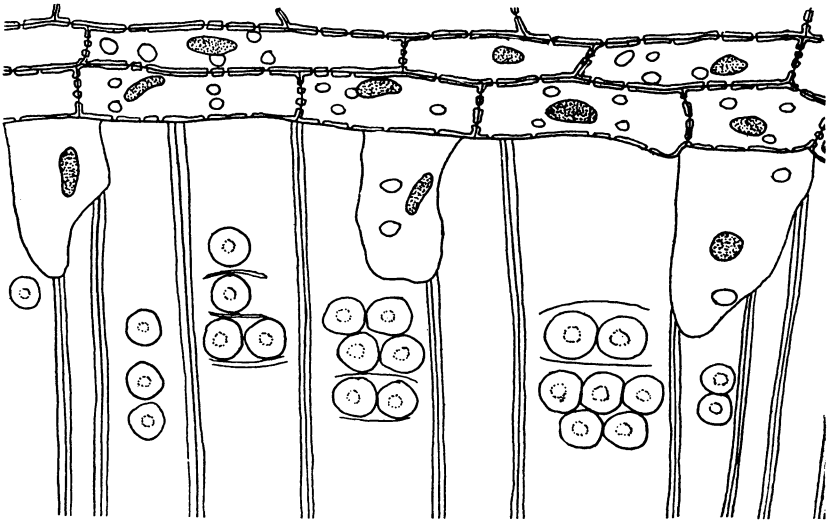

FIG. 3.—*C. libani*, stem; part of a ray traversing three growth rings, at the limit of each of which occurs a marginal parenchyma cell; ×290.

many other genera of conifers. Since calcium oxalate is an end product of katabolism, cells which are charged with it must be regarded as having passed their active or functional stage. This observation together with others here recorded indicate that the marginal cells are in process of degeneration and disappearance.

In order to determine if possible the order of appearance of the structures found at the margin of a ray, serial sections of young stems and roots have been studied. Material of seedlings has not been available, so that the study has been confined to roots and branches of an age of six to seven years. In fig. 6 is shown part of

the fifth and sixth annual rings of a branch of *C. libani*. It will be noticed that on the upper side of the ray the first marginal cell is a tracheid, followed at once by parenchyma, and on the lower side a tracheid is followed by a shadowy cell or "ghost," which still shows a faint bordered pit, and is in turn followed by a row of parenchyma cells. It must be admitted that in some cases the first cells to appear on the margin of a ray are parenchyma cells, but the figure shows the prevailing condition. As far as such observations afford evidence, they indicate that marginal tracheids antedate marginal parenchyma, and where only parenchyma is

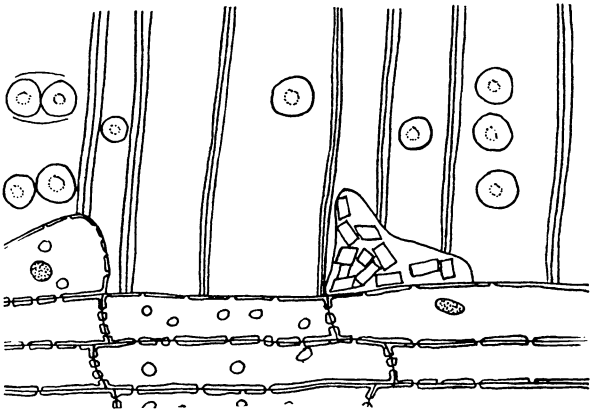

FIG. 4.—*C. libani*, root; a crystal-bearing cell takes the place of starch-bearing parenchyma at the limit of growth ring; ×290.

present it may be inferred that the earlier stages have been passed over.

In a number of cases it has been observed that marginal parenchyma cells are closely associated with resin cells. It will be recalled that in the genus *Cedrus* the resin cells occur on the outer face of the summer wood, and that it is at the limit of an annual ring that marginal parenchyma is most frequent. Fig. 7 shows the close relation of a row of resin cells to parenchyma cells of a ray in a branch of *C. atlantica*. It will be observed that the resin cell in view does not pass behind the ray, but that its end abuts against a marginal parenchyma cell which lies at the outer edge of a layer of summer wood, giving the appearance of a row of resin cells

forming a continuation or outgrowth of a marginal parenchyma cell. Such appearances are fairly common in all three species of *Cedrus*. These observations may throw some light on the origin of the marginal parenchyma. THOMPSON (**8**) in his account of the marginal parenchyma which occurs sparingly in *Abies* suggests that these cells have arisen in connection with the demand for food storage which occurs at the close of the growing season. The close association of marginal parenchyma with resin cells in *Cedrus* suggests, however, that the two structures may have arisen at the same

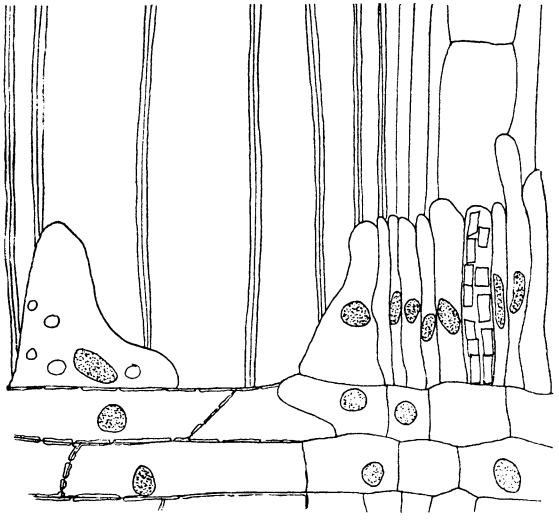

FIG. 5.—*C. libani*, root; one of the erect cells bears crystals; ×290.

time, or even that the vertically elongated marginal parenchyma cells gave rise to rows of resin cells. Of the different positions occupied by resin cells, the terminal position found in *Cedrus* appears to be the original one; at any rate, the plastic materials for supplying such cells are more abundant at the close of the growing season than at any other time. If we consider a marginal cell just cut off from the cambium, it is easy to see that if such cell is in contact with a resin cell which is being supplied with material from the medullary ray, the marginal cell will have a tendency to remain alive rather than thicken its wall and die, that is, develop into a marginal tracheid.

From a number of the observations here recorded the inference seems unavoidable that marginal cells in the genus *Cedrus* are in a vanishing condition. Such observations are: the scattered occurrence of marginal cells, varying from an almost continuous row to occasional cells; persistence of the erect cells of the phloem in line with a few scattering marginal cells on the xylem portion of a ray; the tapering or tailed shape of the cells; occurrence of

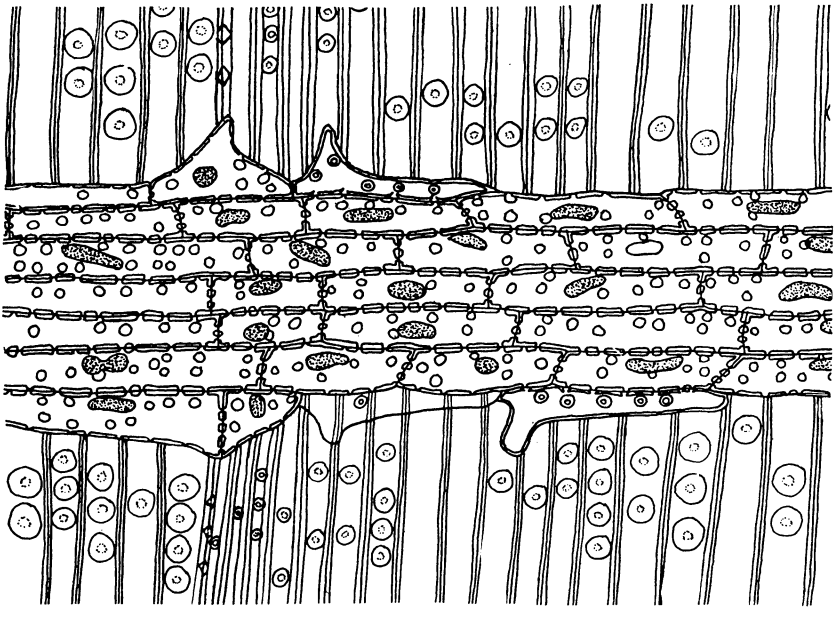

FIG. 6.—*C. libani*, stem; part of the fifth and sixth growth rings, showing earlier appearance of ray tracheids than parenchyma; ×290.

crystal-bearing cells in place of tracheids or starch-bearing parenchyma; occurrence of shadowy cells or "ghosts"; the capricious occurrence of marginal tracheids, as pointed out by STRASBURGER. If then the marginal cells are disappearing, *Cedrus* would appear to show reduction from some such genus as *Pinus* or *Picea*. The foliage of *Cedrus* suggests a relation to *Pinus*, while the cone bears more resemblance to that of *Abies*. The relation to *Pinus* is further indicated by the observation of JEFFREY (2) that when traumatic resin canals are induced in *Cedrus* they occur in both

the vertical and the horizontal plane, while in *Abies* they occur only in the vertical plane. Moreover, resin canals occasionally occur in the xylem of the cone in *Cedrus*, but not in *Abies*.

The foregoing facts go to show that *Cedrus* is in many respects intermediate between *Pinus* and *Abies*. That *Abies* stands farther

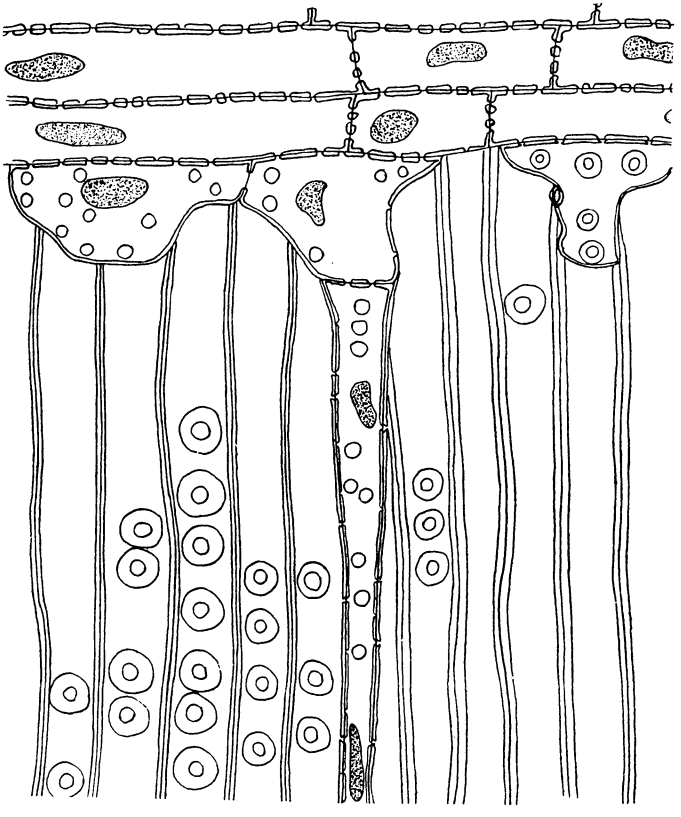

FIG. 7.—*C. atlantica*, stem; at the junction of two growth rings a row of resin cells forms a continuation of a marginal cell of the ray; ×425.

down than *Cedrus* in this reduction series is indicated by the fact that it is mostly in connection with wounds that marginal parenchyma occurs in *Abies*, while such cells occur normally in *Cedrus*. The following evolutionary stages in ray structure are indicated:

1. Medullary rays typically provided with marginal row of cells, which are tracheids: *Pinus*, *Picea*.

2. Marginal row consists of tracheids, but these are replaced by parenchyma at the limit of annual rings: *Cedrus*.

3. Many of the marginal tracheids have been replaced by parenchyma, or have degenerated into ghosts, or have disappeared: *Cedrus*.

4. Marginal cells typically absent, but occur sporadically, especially as a result of injury: *Abies*.

Cedrus shows itself to be a particularly plastic genus, not only in the lack of uniformity of its ray structure, but in its response to wounding, as shown by JEFFREY (2). It would be interesting to ascertain whether wounded material shows reversionary stages in the rays, but my material affords no evidence on this point. In marked contrast to *Cedrus* in this respect is the nearly related *Pseudolarix*. In no part of this plant which has come under my observation has any appearance of ray tracheids been observed, and JEFFREY (*loc. cit.*) remarks upon the absence of wound reactions.

The foregoing observations afford no support to the contention of PENHALLOW that marginal tracheids have been derived from parenchyma. Nor can we agree with his statement (4, p. 107) "the rare occurrence of tracheids in *Thuja*, etc., is to be interpreted as the first evidence of a tendency in development which is only fully realized at a later period." Since these words were written evidence has been accumulating which shows that the series must be read in the opposite direction, and that the sporadic occurrence of ray tracheids in the Cupressineae represents the last stage in disappearance of these cells. The chief evidence in this connection has been supplied by JEFFREY in his study of wound reactions, e.g., in *Cunninghamia* (3) and the observations on the rays of *Cedrus* point in the same direction. Further, there are physiological grounds for opposing the view quoted above, for it is easy to see how a complete row of marginal tracheids can function in carrying water radially, but a few scattered tracheids on the margin of a ray, e.g., of *Thuja*, must be entirely useless, and hence are better regarded as vestigial structures which point back to the time when the ancestors of *Thuja* had a functional row of marginal tracheids. Again, the writer has previously shown (1) that in *Juniperus*, a genus which like *Thuja* shows occasional marginal tracheids, the latter are conterminous with erect cells of the phloem, and erect cells sometimes occur where no marginal tracheids are

to be seen. This appearance is most readily interpreted as a persistence of marginal cells in the phloem after they have disappeared from the xylem.

Summary

1. The medullary rays of *Cedrus* are provided with a margin which varies greatly in composition, being made up of tracheids and parenchyma in varying proportion, or devoid of marginal cells for considerable stretches.

2. Marginal parenchyma when present occurs at the limit of annual rings, and may also extend beyond this point so as to be more plentiful than ray tracheids.

3. The constant occurrence of marginal parenchyma cells at the limit of annual rings, and their close connection with resin cells, indicates that parenchyma has replaced tracheids in connection with secretion of the so-called resin.

4. The marginal cells in *Cedrus* show distinct evidence of being in a degenerating condition.

5. The medullary ray structure confirms the view that *Cedrus* stands intermediate between *Pinus* and *Abies*.

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